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Final Report On Mountain Pine Beetle Population Dynamics and Pheromone Response

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FINAL REPORT ON MOUNTAIN PINE BEETLE POPULATION DYNAMICS AND PHEROMONE RESPONSE

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Introduction

The response of mountain pine beetle (MPB), *Dendroctonus ponderosae*, to the anti-aggregation pheromone verbenone in previous field trials has been inconsistent. Early studies demonstrated a strong anti-aggregation effect in the field (Amman et al. 1989, Lindgren et al. 1988; Gibson et al. 1991). However, reliable stand or tree protection has not been produced (Safranyik et al. 1992, Lister et al. 1990, Bentz et al. 1989). The objective of this study was to examine new and old MPB epidemics and investigate differences between the two population stages in their response to pheromone treatments. Additional data were collected describing differences in individual size, population sex ratio and flight chronology between new and old epidemics.

Methods

In the summers of 1992 and 1993 we conducted pheromone tests with MPB to determine if beetle response to verbenone, ipsdienol and the MPB aggregation pheromone (trans-verbenol, exobrevicomin and myrcene) varied between epidemic populations which were just beginning and those which had been killing trees for several years in the same locality. Our tests were conducted July 17 - August 25, 1992 and August 3 - September 8, 1993 in the Sawtooth National Recreation Area in south central Idaho. In 1992 we tested 12 treatments attached to multiple funnel Lindgren flight traps with 10 different complete blocks, 5 in two areas with new epidemics and 5 in two areas with old epidemics. All 10 areas were located within the same general area < 10 km apart. Treatments were randomized after each collection. Traps were collected daily or several times weekly. Beetles were sexed and measured (pronotal width). Associated insects, mainly other coleoptera but also parasitoid hymenoptera and diptera were all retained in alcohol for analysis. The 12 treatments were:

MPB lure	2x lure	ipsdienol
verbenone	lure + ipsdienol	lure + verbenone
2x lure + ipsdienol	2x lure + verbenone	lure, ipsdienol + verbenone
2x lure, ipsdienol + verbenone	ipsdienol + verbenone	blank control

In 1993 we tested 6 treatments including a host kairomone, methyl chavicol. Our treatments were:

MPB lure	lure & verbenone
MPB lure & methyl chavicol	methyl chavicol
lure & ipsdienol	blank control

Our traps were placed as before in 10 blocks; 5 in areas with new MPB epidemics and 5 in areas with old MPB epidemics. Collected MPB were sexed but not measured in 1993. MPB and associated insects collected in traps were preserved in alcohol for further analyses.

Results

Old vs New pheromone response.

Beetles in new epidemic populations were repelled more strongly by anti-aggregation pheromones (verbenone and ipsdienol) than beetles in old epidemics, in 1993 (Table 1). In 1992 the anti-aggregation effect of verbenone was equal in new and old areas; but ipsdienol had a stronger anti-aggregation effect in new epidemic populations (Table 2).

Beetle response to a repellent host volatile, methyl chavicol (tested only in 1993) was the reverse of the response to pheromones. Beetles in old epidemics avoided methyl chavicol more strongly than beetles in new epidemics (Table 3).

Table 1 Reduction in Catch of mountain pine beetles: anti-aggregants and baits vs. baits alone. SNRA ID. 1992-93.

		1993	1992
verbenone	new	99%	99%
	old	89%	99%
ipsdienol	new	81%	65%
	old	73%	45%
methyl chavicol	new	65%	---
	old	75%	---

Table 2 Catch of mountain pine beetles with semiochemical attractants and interruptants. New vs. Old epidemic populations. Sawtooth NRA. ID. 1992.

New Epidemic Populations

Tmt[1]	x[2]	sd	f[3]	m[4]	N
b	37.9a[5]	(42.2)	7.5a	6.3a	(28)
bi	13.3b	(12.1)	5.6a	4.2b	(28)
bv	0.5c	(0.7)	0.1b	0.3c	(29)
biv	0.2c	(0.4)	0.1b	0.1c	(28)
x	0.2c	(0.5)	0.1b	0.1c	(27)
i	1.7	(5.3)	0.9	0.4	(29)
v	0.6	(1.3)	0.2	0.2	(30)
iv	0.3	(0.6)	0.1	0.2	(30)
bb	38.3	(51.5)	7.6	5.7	(29)
bbi	20.7	(35.9)	5.5	4.8	(28)
bbv	1.3	(3.8)	0.4	0.6	(30)
bbiv	0.3	(0.7)	0.1	0.2	(28)

Old Epidemic Populations

Tmt	x	sd	f	m	N
b	23.4a	(32.1)	6.1a	4.6a	(30)
bi	12.8a	(11.5)	6.3a	3.9a	(28)
bv	0.3b	(0.5)	0.2b	0.1b	(27)
biv	0.5b	(1.2)	0.3b	0.2b	(30)
x	0.2c	(0.8)	0.2b	0.0c	(29)
i	0.5	(1.2)	0.3	0.1	(29)
v	0.5	(1.3)	0.3	0.1	(30)
iv	0.2	(0.5)	0.2	0.0	(29)
bb	36.3	(55.1)	9.2	5.4	(30)
bbi	14.9	(11.8)	6.6	4.8	(28)
bbv	0.4	(1.3)	0.2	0.2	(29)
bbiv	0.6	(0.9)	0.2	0.2	(28)

1 Treatments: b = bait (exobrevicomin, trans-verbenol, myrcene), bb = 2 baits, i = ipsdienol, v = verbenone, bi = bait & ipsdienol, bv = bait & verbenone, bbi = 2 baits & ipsdienol, bbv = 2 baits & verbenone, biv = bait & ipsdienol & verbenone, bbiv = 2 baits & ipsdienol & verbenone, iv = ipsdienol & verbenone, x = blank control

2 mean mountain pine beetle caught

3 mean females caught (subsample ≤ 20 MPB/ trap sexed)

4 mean males caught (subsample ≤ 20 MPB/ trap sexed)

5 Means within a column followed by different letters are significantly different; Kruskal-Wallis Test on ranks; $\alpha = 0.05$

Table 3 Catch of mountain pine beetles with semiochemical attractants and interruptants. New vs. Old epidemic populations. Sawtooth NRA. ID. 1993.

New Epidemic Populations

Tmt[1]	x[2]	sd	f[3]	m[4]	N
b	21.1a	(39.0)	8.6a	3.8a	(34)
bm	7.3b	(11.6)	3.9b	1.6b	(33)
bi	4.1c	(6.8)	2.2c	1.1c	(33)
bv	0.2d	(0.5)	0.1d	0.1d	(32)
x	0.2d	(0.8)	0.1d	0.1d	(32)
m	0.0d	(0.2)	0.0d	0.0d	(30)

Old Epidemic Populations

Tmt	x	sd	f	m	N
b	34.3a	(55.3)	7.5a	3.5a	(31)
bm	8.6ab	(13.7)	4.6a	1.6a	(26)
bi	9.2b	(11.9)	5.3a	2.1a	(27)
bv	3.8c	(11.3)	1.7b	0.6b	(28)
x	0.6c	(0.9)	0.4c	0.2	(29)
m	0.4c	(1.1)	0.3c	0.1	(27)

1 Treatments: b = bait (exobrevicomin, trans-verbenol, myrcene), bm = bait & methyl chavicol, bi = bait & ipsdienol, bv = bait & verbenone, m = methyl chavicol, x = blank control

2 mean mountain pine beetle caught

3 mean females caught (subsample ≤ 20 MPB/ trap sexed)

4 mean males caught (subsample ≤ 20 MPB/ trap sexed)

5 Means within a column followed by different letters are significantly different; Kruskal-Wallis Test on ranks; $\alpha = 0.05$

Verbenone reduced the catch of MPB in traps by 99% in all but the 1993 old epidemic where the reduction was only 89% (Table 1). Ipsdienol reduced the catch of MPB by 45% - 81% (Table 1). In both 1992 and 1993 the reduction in catch was greater in new epidemic populations (65% and 81%, respectively) than in old epidemic populations (45% and 73% reduction, respectively). Verbenone and ipsdienol combined never significantly reduced the catch below the level of verbenone alone with bait (Table 2). However, in new populations the combination of ipsdienol and verbenone with either single or double baits did produce a nonsignificant trend towards lower catches than the combination of only verbenone and baits. A similar reduction was not observed in old epidemic populations.

In 1992 catches were 21% larger, on average, than the same treatments in 1993.

Beetle size, population stage and pheromone response

Beetles in new populations were larger than beetles in old populations (Table 4). This was true for both males and females from the new population compared against males and females, respectively, from the old population. T-tests comparing beetle size from old and new areas for both sexes show significant differences ($p < 0.0001$ for each sex).

Table 4 Beetle Size and Population Stage SNRA,ID. 1992

	Block	female mean size[1]	rank	male mean size	rank
old	Upper Pole Creek	2457	9	2236	9
	Lower Pole Creek	2423	10	2217	10
	Alturas Jct.	2522	6	2291	6
	Alturas Creek	2464	8	2260	7
	Alturas Sale	2476	7	2244	8
new	Upper French Creek 1	2532	5	2303	4
	Lower French Creek	2543	3	2305	3
	Lower Smiley Creek	2570	1	2296	5
	Upper Smiley Creek	2540	4	2309	2
	Venice	2551	2	2343	1

1 Micrometer units

There was an inverse relationship between the mean size of beetles (by sex) and the attractiveness of the treatment (Table 5). For both new and old populations taken together the largest mean size of males and females was found in the least attractive trap, the blank control. The next four largest mean beetle sizes of both sexes were found in treatments which for both old and new epidemics were among the least attractive. For males these treatments all included verbenone. For both old and new epidemics the 4 most attractive treatments (more attractive by an order of magnitude over other treatments) had small mean beetle sizes, in the lower 50% for both sexes. These were the treatments: b, bb, bbi and bi. No verbenone was present in these most attractive treatments.

Table 5 Rank of mean size by sex, and mean catch for mountain pine beetles in traps with semiochemical treatments. Sawtooth NRA. ID. 1992

Tmt[1]	mean catch new pop'n	mean catch old pop'n	mean size of females[2]	rank[3]	mean size of males	rank
bb	38.3	36.3	2.506	7	2.282	10
b	37.9	23.4	2.511	10	2.275	8
bbi	20.7	14.9	2.557	8	2.178	9
bi	13.3	12.8	2.511	12	2.308	7
i	1.7	0.5	2.490	2	2.285	12
bbv	1.3	0.4	2.497	3	2.291	2
v	0.6	0.5	2.510	9	2.279	4
bv	0.5	0.3	2.545	11	2.341	6
bbiv	0.3	0.6	2.540	6	2.295	11
iv	0.3	0.2	2.524	5	2.266	3
biv	0.2	0.5	2.533	4	2.310	5
x	0.2	0.2	2.562	1	2.383	1

1 Treatments: b = bait (exobrevicomin, trans-verbenol, myrcene), bb = 2 baits, i = ipsdienol, v = verbenone, bi = bait & ipsdienol, bv = bait & verbenone, bbi = 2 baits & ipsdienol, bbv = 2 baits & verbenone, biv = bait & ipsdienol & verbenone, bbiv = 2 baits & ipsdienol & verbenone, iv = ipsdienol & verbenone, x = blank control

2 Micrometer units

3 Largest - smallest = 1 - 12

Beetle size and flight day

Larger beetles of both sexes flew during the first week of the flight period (July 17-23, 1992). Smaller beetles of both sexes flew during the third week of flight (July 31 - August 8, 1992). These differences were significant (t-test $\alpha = 0.05$ $p < 0.0001$ for each sex Table 6). Amman and others have noted the early emergence of large beetles previously and related it to greater phloem thickness.

Table 6 Flight day and mean size of mountain pine beetles captured in flight traps with semiochemicals. SNRA, ID. 1992

Calendar day	Flight day	mean size of females[1]	rank[2]	mean size of males	rank
July 17	1	2497	6	2315	4
July 18	2	2590	2	2320	3
July 19	3	2603	1	2350	2
July 20	4	2586	3	2358	1
July 23	5	2528	4	2273	6
July 25	6	2457	8	2274	5
July 27	7	2513	5	2262	8
July 28	8	2480	7	2248	9
July 31	9	2477	9	2240	11
August 3	10	2391	13	2241	10
August 5	11	2408	11	2228	12
August 7	12	2392	12	2204	13
August 8	13	2418	10	2165	7

1 Micrometer units

2 Largest - smallest = 1 - 12

Beetle sex and treatments: new vs old populations

Overall, traps in both new and old areas in both 1992 and 1993 caught more females than males (Table 7). In both years there was a higher proportion of females overall in the old area than in the new (F/M ratio 1992 old: 1.57, new: 1.43; 1993 old: 2.56, new: 2.25). In both years blank control traps caught more males than females in new populations and more females than males in old areas.

In both years verbenone caught more males than females in new populations but more females than males in old populations. This trend was seen in all 7 treatments that contained verbenone in both years. In new populations all verbenone treatments caught more males than females despite the overall female bias of the total population captured. In old populations all but one treatment which contained verbenone caught more females than males.

Ipsdienol alone caught substantially more females than males in both new and old populations in 1992. Ipsdienol alone was not tested in 1993.

Table 7 Beetle sex ratio (F/M) by treatment: new vs. old population stage

	1992		1993	
	new	old	new	old
Tmt[1]	ratio	ratio	ratio	ratio
overall	1.43	1.57	2.25	2.56
x	0.63	5.05	0.75	2.40
b	1.49	1.42	2.27	2.43
bi	1.3	1.6	2.05	2.59
bv	0.39	2.0	0.74	2.98
m	--	--	0	2.34
bm	--	--	2.46	3.08
bb	1.57	1.75	--	--
i	2.61	2.43	--	--
v	0.70	3.7	--	--
bbi	1.26	1.32	--	--
bbv	0.60	1.16	--	--
biv	1.0	1.3	--	--
bbiv	0.6	0.45	--	--
iv	0.63	5.05	--	--

1 Treatments: b = bait (exobrevicomin, trans-verbenol, myrcene), bb = 2 baits, i = ipsdienol, v = verbenone, bi = bait & ipsdienol, bv = bait & verbenone, m = methyl chavicol, bm = bait & methyl chavicol, bbi = 2 baits & ipsdienol, bbv = 2 baits & verbenone, biv = bait & ipsdienol & verbenone, bbiv = 2 baits & ipsdienol & verbenone, iv = ipsdienol & verbenone, x = blank control

Discussion

Taken together these results document biologically significant differences in early and late stages of mountain pine beetle epidemics. The variation in response of new and old populations to pheromones may partly explain the inconsistent results obtained with the antiaggregation pheromone verbenone. Inconsistent protection by verbenone may also be related to differences in verbenone sensitivity between early flying colonists and later mass attack participants. The earliest beetles to fly (and hence the most likely primary colonists of new host trees) in our tests were the larger beetles. Larger beetles were more likely to be found in traps with verbenone as part of the treatment.. i.e. verbenone did not repel large beetles as effectively as smaller beetles. Verbenone very effectively reduced the attraction of smaller beetles that flew later to baited traps; but it appears it is less likely to inhibit the colonizing larger beetles. This behavior (early verbenone tolerance or attraction and later verbenone avoidance) may be determined by internal physiological state (fat reserves etc..). It would seem to be adaptive in that early colonists should benefit if they can use verbenone to help locate trees in the initial stages of colonization. Later participants in a mass attack would benefit if they could use verbenone to avoid overcrowded hosts.

Once a tree is partially colonized and pheromone production begins, the attraction may be so great as to overwhelm the later anti-aggregation effect of artificial verbenone treatments. This interpretation is supported by observations of fire-scorched, verbenone treated trees in experiments conducted by Amman. In these tests, with wet cool weather, verbenone treated trees were generally the first trees to receive some attacks. In natural epidemic situations the preliminary attacks of the larger, less verbenone sensitive colonizing beetles may be a fatal breach of tree defense which precedes the overwhelming and all but unstoppable mass attack. In this scenario host repellents, such as methyl chavicol, that are not produced by beetles during attack initiation may be more important than verbenone in avoiding initial colonization leading to mass attack.

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Expected Publications from this Work:

Hobson, Kenneth R., R.A. Werner and A.T. Whitehead. Methyl chavicol: a possible ecological and olfactory link between host stress and host selection by bark beetles. *in prep.*

Hobson, Kenneth R. and G.D. Amman. Why verbenone doesn't always work: an hypothesis of beetle quality. *in prep.*